American Fern Journal 75(1):22–28 (1985)

Special Report

The Present Evolutionary and Taxonomic Status of the Fern Genus *Polystichum*: The 1984 Botanical Society of America Pteridophyte Section Symposium

DAVID S. BARRINGTON
Department of Botany, University of Vermont, Burlington, VT 05405

The fern genus *Polystichum* has presented major problems in definition and circumscription of species since its description by Roth in 1799. Part of the problem is the vast diversity within the genus: the number of species is reported as more than 175 by Copeland (1947). In addition, hybridization is extremely common (Knobloch, 1976), and agamospory has been reported among experimental plants from Europe (Vida & Reichstein, 1975). There is also substantial evidence of phenotypic and ontogenetic variability within species of the genus. Good progress has been made in solving evolutionary and taxonomic problems in the north-temperate and boreal regions (Manton, 1950; Manton & Reichstein, 1961; Kurata, 1964; Sleep & Reichstein, 1967; Daigobo, 1972; W. Wagner, 1973; D. Wagner, 1979); however, little taxonomic and virtually no evolutionary work has been done on the genus in tropical or austral regions. Hence this large genus of dryopteroid ferns is in need of substantial attention from systematic and evolutionary biologists, especially in tropical regions.

Christopher Haufler at the University of Kansas organized a symposium on *Polystichum* for the American Institute of Biological Sciences meetings in Fort Collins, Colorado, during August of 1984. As Haufler noted in his opening remarks, the purpose of the symposium was to draw attention to a complex and poorly understood genus of ferns, rather than to solve problems by consensus of the speakers. Participants in the symposium focused on the evolutionary problems encountered in New World *Polystichum*, primarily from a taxonomic and floristic viewpoint. This paper summarizes the Fort Collins symposium.

MORPHOLOGICAL VARIATION AND EVOLUTION IN *POLYSTICHUM*

Warren H. Wagner, Jr.—University of Michigan

The systematic problems in the genus *Polystichum* are best placed in the context of the structural variation evident at different taxonomic levels. The genus as a whole is typical of the Polypodiales in having a suite of diagnostic features none of which is universal: terrestrial habit; medium stature; short-creeping and scaly rhizome; lustrous, coriaceous, once- to twice-pinnate, free-veined, anadromous blades; pinna (pinnule) margins more or less spinulose;

indusium abaxial and peltate; spores bilateral and monolete; perispore well-developed; haploid chromosome number of 41 or a multiple thereof. Transformation of diagnostic features (such as loss of the peltate indusium) has led to problems in definition of *Polystichum* as well as the description of various segregate genera, which may or may not represent monophyletic groups. In *Polystichum*, as in many fern genera, definition of a group and its component species has been based on subjective arguments such as those from tradition, authority, and consistency—rather than from arguments based on objective documentation and analysis of the variation in structure throughout the group.

Several of the genera segregated from *Polystichum* are in need of critical re-evaluation. *Plecosorus*, known from Mexico to Panama, differs only in lacking a true indusium (common in *Polystichum*) and having a modified, recurved margin protecting the sporangia (false indusium). *Papuapteris* of New Guinea shares both of the critical features of *Plecosorus*, presumably as homoplasies. New World taxa placed in *Phanerophlebia* or *Cyrtomium* have broad lamina segments provided with irregularly anastomosing veins (not with regularly anastomosing veins with included veinlets as in true Old World *Cyrtomium*) but are otherwise typical members of *Polystichum*. Hybrids of other genera and *Polystichum* are now known. Most dramatic is the hybrid between *Dryopteris goldiana* and *Polystichum lonchitis* from Ontario, on which the University of Michigan pteridologists are currently working. *Polystichum* and its allied genera constitute an array of evolutionary groups that have maintained at least partial genetic homology in spite of isolation and independent evolution.

Hybridization and polyploidization commonly generate reticulate complexes in *Polystichum*. However, a series of plants that appear to be hybrids may actually be the products of divergence. One newly documented complex from Hawaii comprises a group of three bipinnate species that are similar in leaf dissection and general aspect, but differ in chromosome number ($n = 41$, 82, and 164), leaf and segment shape, habitat preference, and scale structure.

Within species, structural features can be highly variable. Numerous trivial forms of the well-known eastern North American *Polystichum acrostichoides* have been reported and described. A peculiar environmental factor has been pinpointed as responsible for the derivation of forma *incisum* (Gray) Gilbert, which has variously pinnatifid pinnae instead of typical serrulate pinnae on leaves produced late in a season on damaged plants bearing otherwise typical foliage (W. Wagner et al., 1970). Such striking short-term alterations demonstrate that, in *Polystichum*, variations may be superficial and should be tested.

Polystichum in Temperate and Boreal North America

David H. Wagner—University of Oregon

Polystichum is depauperate in eastern North America (four species, one of which is endemic), but more diverse in the West (13 species, nine of which are endemic). A hypothesis for a reticulate complex involving 11 of the species is based on an analysis of the sexual species and seven known sterile hybrids (W. Wagner, 1973; D. Wagner, 1979). From the seven basic diploid species, five tet-

raploids and one hexaploid have been generated in nature. All but one of the six needed diploid (or tetraploid) progenitors are known. Though fragmentary specimens presumed to represent the sixth, a second progenitor for *P. andersonii*, are on hand, better documentation (complete plants, cytological analysis, or hybrid synthesis) is needed.

Despite the current good resolution of the complex, individual specimens are frequently difficult to identify from diagnostic keys. The difficulty may be better understood with reference to Vavilov's "Law of Homologous Series in Variation" (Vavilov, 1922). Based on exhaustive studies of crop plants, Vavilov concluded that closely allied species are characterized by similar and parallel series of hereditary variations. In *Polystichum*, parallel series of hereditary variations are evident in ontogenetic series among the species with divided fronds. For example, a juvenile frond of *P. braunii* (fully bipinnate at maturity) is less divided than a mature frond of *P. setigerum*, which is merely bipinnatifid at maturity. When plants are under environmental stress, leaf development is arrested in a juvenile, stunted condition, although sori may still be produced. For example, the tetraploid *Polystichum scopulinum* growing in exposed sites at high elevations closely mimics the tetraploid *P. kruckebergii*, with which it shares a set of chromosomes contributed by the diploid *P. lemmonii*. Hybrid taxa, whether fertile species or sterile hybrids, approach parental extremes in variation when growing in a habitat typical of one parent.

The most nearly parallel series of variations is found in the two sibling species, *P. munitum* and *P. imbricans*. Although consistently ecologically distinct, the two are often found in contiguous habitats and hybridize frequently. The hybrids are sterile, as shown by cytological analysis. Continuing studies of these two species should be of great interest, since our understanding of divergent speciation in the ferns lags behind our understanding of polyploidization as a route to new species.

Polystichum in the West Indies

John T. Mickel—New York Botanical Garden

West Indian *Polystichum* is the most distinctive element in the New-World *Polystichum* flora. Nevertheless, it has received attention only twice: Maxon's (1909, 1912) classic revisionary work and Morton's (1967) study of the Cuban species. Seventeen of the 30 known species are once pinnate, and 14 are proliferous; both of these traits are rare on the mainland (though common in Japan and the Himalayas). Cuba, Jamaica, and Hispaniola constitute the center for the West Indian group: 25 of the 30 species are endemic there, whereas only three of the species reach Puerto Rico and two the Lesser Antilles. Only two species, *P. muricatum* and *P. platyphyllum*, are found both in the West Indies and in continental Latin America. Both are widespread species of low and middle elevations. Many of the West Indian species are limited to calcareous rock and soils, which is doubtless a critical determinant in their geographic distribution.

Wherever *Polystichum* has been studied in detail, hybridization has been shown to play an important role in speciation. Preliminary study suggests that

the West Indian taxa are no exception. Chromosome counts have been made for only six species (Walker, 1966). However, analysis of gross structural features of the sporophytes, as well as of spore-surface structure and spore-shape irregularities, when taken together with the few cytological records, demonstrates that there are at least six sterile hybrids and four tetraploid nothospecies among West Indian *Polystichum*.

Polystichum in Mexico

Alan R. Smith—University of California, Berkeley

Recent floristic work has provided the first modern treatments of *Polystichum* for the southern limits of the North American continent (Smith, 1981; Stolze, 1981). The genus in northern Latin America comprises about sixteen species, mostly confined to southern Mexico. Four species groups can be discerned. The largest group, comprising nine species (all of which are bipinnate, indusiate, and grow at middle to high elevations) has its affinities with the *P. setiferum* group (section *Metapolystichum* of Daigobo, 1972). The second group is of two north-temperate species at the southern limits of their ranges: *P. munitum* from Isla Guadelupe and *P. acrostichoides* from Nuevo Leon. The third group has a single representative, the rare *P. munchii*, closely allied to the West Indian *P. echinatum*. Like many of its West Indian allies, *P. munchii* is limited to limy substrates. A fourth group of four species has affinities farther south in continental Latin America. Two, *P. polyphyllum* and *P. speciosissimum*, are exindusiate species from high elevations; the other two, *P. platyphyllum* and *P. mickelii*, occur in low to mid-elevation rain forests. Seven of the Mexican species have been examined cytologically. Four counts are diploid ($n = 41$); *P. fournieri* and *P. polyphyllum* are tetraploid ($n = 82$); and *P. platyphyllum*, probably a species complex, has both cytotypes. In northern Latin America, it appears that species infrequently grow together, and interspecific hybridization has not been documented.

Polystichum in Central and South America

David S. Barrington—University of Vermont

Polystichum in Central and South America can be divided into two geographical and evolutionary groups, one tropical and the other austral. The austral group has received some attention (Christ, 1893, 1905; Looser, 1968), but the tropical one has not until quite recently (Barrington, 1985).

The situation in Costa Rica is best known, where the genus is represented by six species above 2800 m. Two are at the southern limit of their range (diploid *P. speciosissimum* and tetraploid *P. fournieri*) and two others are common throughout the mountains of the New World tropics (diploid *P. lehmannii* and tetraploid *P. polyphyllum*). In addition, two species are apparently endemic, an undescribed diploid and an undescribed tetraploid. Three hybrids have been

found, including a sterile triploid (with 41 pairs and univalents) between the two endemic species and a sterile triploid between the endemic tetraploid and some unknown diploid progenitor allied to *P. polyphyllum*. The two endemic species appear to be an allotetraploid and one of its diploid progenitors based on chromosomal evidence, morphology, and preliminary electrophoretic analysis (C. H. Haufler, pers. comm.). Secondary interaction in the Sierra Talamanca of Costa Rica appears to be promoted by human disturbance, because the hybrids all occur in disturbed sites, and the progenitor species are found in proximity most often along roadcuts and in pastures and disturbed cloud forest and alpine areas.

Preliminary work in northern South America suggests that there are few species and that hybrids are not common. At high elevations, two broad-ranging species are common: *P. lehmannii* (along open streambanks) and *P. polyphyllum* (throughout the páramo). In upper-elevation cloud forests, there is a suite of locally endemic and mostly undescribed species (mostly from the moist margins of small streams). At middle elevations, the broad-ranging *P. platyphyllum* grows with the locally common *P.* (or *Cyrtomium*) *dubium*. In one mixed population of the two in Ecuador, there are plants with an array of features intermediate between *P. dubium* and *P. platyphyllum* that resemble the type of *P. dictyophyllum*. Spores of these intermediates are irregular, allowing the suggestion that at least some plants assignable to *P. dictyophyllum* are hybrids between *P. dubium* and *P. platyphyllum*. Further study of this trio should provide better understanding of the relationship of the anomalous *P. dubium* to the rest of *Polystichum*. At low elevations, the broad-ranging *P. muricatum* is found as far south as Ecuador. This diploid species is peculiar in that sori often abort before maturity, though regular spores are produced during meiosis. Reniform indusia at some sori are a second unusual feature of *P. muricatum*.

Summary

In the New World, there are five recognizable elements in *Polystichum*: the highly reticulated boreal–north temperate element (affinities circumboreal); the Mexican element (affinities warm–temperate Asian); the Antillean element (affinities in Southeast Asia and the western Pacific); the Andean element (affinities unclear); and the Austral or South Andean element (affinities austral, including New Zealand and Australia). All of these but the Austral element received some attention in this symposium; all need further scholarly attention. The symposium speakers noted in the discussion that followed the presentations that multiple origin of analogous character states is particularly common in *Polystichum*: for example, the true indusium has been lost in three of the five elements of the flora, the Antillean, the Andean, and the Austral.

Polystichum species, defined on both morphological and cytological grounds, have characteristic habitats and elevational preferences. Hybridization typically yields sterile hybrids and new species via polyploidization, both in north-temperate areas and in montane tropics. However, in the tropics, hybridization appears to be localized: the Greater Antilles and Costa Rica are rich in hybrids, whereas other parts of the Neotropics have not yet yielded many hybrids. Either

hybrids remain to be detected in these other regions, or further inquiry may allow a new understanding of what promotes hybridization in the genus.

All of the contributors to the symposium agreed that variability, especially ontogenetic and phenotypic but also in response to perturbation of individual plants, has played an important role in confusing specialists in the group. The usual duplication of names provided by specialists working in isolation on conspecific plants has been complicated by the peculiar reduction of the vast majority of bipinnate *Polystichum* species to a few taxa, initiated by Hooker (1862) and maintained by Christensen (1905–6).

Students of *Polystichum* have before them the substantial task of providing monographic treatments for tropical American groups. In addition, there remains the task of identifying phylogenetic groups above the species level among New World *Polystichum*.

Literature Cited

Barrington, D. S. 1985. The morphology and origin of a new *Polystichum* hybrid from Costa Rica. Syst. Bot. 10:199–204.

Christ, H. 1893. Les différentes formes de *Polystichum aculeatum* (L. *sub Polypodio*), leur groupement et leur dispersion, y compris les variétés exotiques. Ber. Schweiz. Bot. Ges. 3:26–48.

———. 1905. Uber die australen *Polystichum*-Arten. Ark. Bot. 4(12):1–5.

Christensen, C. 1905–6. *Index filicum*. Copenhagen: Hagerup.

Copeland, E. B. 1947. *Genera filicum*. Waltham, Mass.: Chronica Botanica.

Daigobo, S. 1972. Taxonomical studies on the fern genus *Polystichum* in Japan, Ryukyu, and Taiwan. Sci. Rep. Tokyo Bunrika Daigaku, Sect. B. 15(224):57–80.

Hooker, W. J. 1862. *Species filicum*. Vol. 4. London: W. Pamplin.

Knobloch, I. W. 1976. Pteridophyte hybrids. Publ. Mus. Michigan State Univ. Biol. Ser. 5:277–352.

Kurata, S. 1964. On the Japanese ferns belonging to the *Polystichum polyblepharum* group. Sci. Rep. Yokosuka City Mus. 10:17–41.

Looser, G. 1968. Los helechos del genero *Polystichum* Roth en Chile: notas preliminares. Anales del Museo de Historia Natural 1:49–58.

Manton, I. 1950. *Problems of cytology and evolution in the Pteridophyta*. Cambridge: Cambridge Univ. Press.

——— and T. Reichstein. 1961. Zur Cytologie von *Polystichum braunii* (Spenner) Fée und seiner Hybriden. Ber. Schweiz. Bot. Ges. 71:370–383.

Maxon, W. R. 1909. A revision of the West Indian species of *Polystichum*. Studies in Tropical American Ferns 2. Contr. U.S. Natl. Herb. 13:25–38.

———. 1912. Further notes on the West Indian species of *Polystichum*. Contr. U.S. Natl. Herb. 16:49–51.

Morton, C. V. 1967. Studies of fern types. I. Contr. U.S. Natl. Herb. 38:29–83.

Roth, A. W. 1799. Auszug eines Briefes von Hrn. Prof. Mertens in Bremen an den Herausgeber. Arch. Bot. (Leipzig) 2(1):103.

Sleep, A. and T. Reichstein. 1967. Der Farnbastard *Polystichum meyeri* hybr. nov. = *Polystichum braunii* (Spenner) Fée × *P. lonchitis* (L.) Roth und seine Cytologie. Bauhinia 3:299–309, 363–374.

Smith, A. R. 1981. Part II. Pteridophytes. In *Flora of Chiapas*, ed. D. E. Breedlove. San Francisco: California Acad. of Sciences.

Stolze, R. G. 1981. Ferns and fern allies of Guatemala. Part 2. Polypodiaceae. Fieldiana, Bot. n.s. 6:1–522.

Vavilov, N. I. 1922. The law of homologous series in variation. J. Genet. 12:48–89.

Vida, G. and T. Reichstein. 1975. Taxonomic problems in the fern genus *Polystichum* caused by

hybridization. Pp. 126–135 in *European floristic and taxonomic studies*, ed. S. M. Walters. Faringdon: E. W. Classey.

WAGNER, D. H. 1979. Systematics of *Polystichum* in western North America and north of Mexico. Pteridologia 1:1–64.

WAGNER, W. H., JR. 1973. Reticulation in Holly Ferns (*Polystichum*) in the western United States and adjacent Canada. Amer. Fern J. 63:99–115.

———, D. R. FARRAR, and B. W. MCALPIN. 1970. Pteridology of the Highlands Biological Station area, southern Appalachians. J. Elisha Mitchell Sci. Soc. 86:1–27.

WALKER, T. G. 1966. A cytotaxonomic survey of the pteridophytes of Jamaica. Trans. Royal Soc. Edinburgh 66:169–237.

SHORTER NOTES

***Marsilea quadrifolia* and *M. vestita* in the Floras of Kansas and Missouri.**— In the fern floras of both Kansas and Missouri two species of water-clover ferns, *Marsilea*, have been recognized: a native species, *Marsilea vestita* Hook. & Grev., and the introduced Eurasian *M. quadrifolia* L. *M. vestita* is common in central and western Kansas, while *M. quadrifolia* has been reported from only two counties in the southeastern part of the state (Petrik-Ott, Nova Hedwigia Beih. 61:1–332, 1979). In Missouri, both species have been reported from a single county each: *M. vestita* (as the synonym *M. mucronata* A. Braun) from Barton County in southwestern Missouri and *M. quadrifolia* from Platte County in northwestern Missouri (Steyermark, Flora of Missouri, Iowa State University Press, Ames, 1963). On the basis of specimens known at present, however, *Marsilea quadrifolia* should be deleted from the flora of Kansas and *M. vestita* should be deleted from the flora of Missouri. The latter is particularly of note as this species has been listed as endangered in Missouri.

Petrik-Ott (op. cit.) reported *M. quadrifolia* from Kansas on the basis of two specimens, both from the herbarium of the University of Kansas (KANU): *Kolstad & Harms 1581* from Cherokee Co., and *Holland 1993* from Neosho Co. The reasons for this are unclear as both sheets are annotated as *M. vestita* by Petrik-Ott, and the only mention of *M. quadrifolia* on either sheet is on the original label of *Holland 1993*. An additional specimen (*Harms 1137*, KANU) from Cherokee Co. was not cited by Petrik-Ott but was annotated by her as *M. quadrifolia*; this specimen has characters of sporocarp pedicel length (7 mm), position of attachment of this pedicel (4 mm above the petiole base), and glabrate sporocarps that are characteristic of *M. quadrifolia*. The specimen also has, however, asymmetrical abaxially hairy leaflets that are longer than wide and have concave inner margins and slightly crenulate terminal margins. In addition, the rhizomes are 1.0 mm or less thick and lack roots in the internodes. These are all characters of *M. vestita*, which normally has short-pedicelled (2–3 mm), basally attached hairy sporocarps.